The response of macroinvertebrates to artificially enhanced detritus levels in plantation streams

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Abstract

The leaves and wood from vegetation surrounding headwater streams constitute a major food source for aquatic invertebrates, providing they are retained upon the streambed and not transported downstream. This study investigated the response of aquatic invertebrates to artificially increased detritus retention, in an effort to reproduce the naturally occurring build up of dead organic matter associated with streams in old-growth forest. The background detrital standing stock in streams in Kielder Forest (Northumberland, UK) was low, approximately 32 gm^{-2}. Two streams flowing through dense conifer plantation and one in open broadleaved woodland were manipulated by the addition of logs over a 10 m stream reach. After several months, log addition significantly enhanced detrital standing stocks in both conifer and broadleaved streams. Total invertebrate abundance, taxon richness and the numbers of certain numerically dominant families were significantly higher in experimental than reference reaches in both conifer and broadleaved streams. This response was most marked for detritivores, whilst non-detritivore groups often showed no response to the manipulation. Whilst in the short term the responses to enhanced retention may reflect a redistribution of the local fauna, it is argued that over a longer time-scale, a genuine increase in invertebrate density and diversity could occur. Allowing old-growth forest to develop in planted valley bottoms may be a viable management option for conservation. If established alongside streams, it would ensure continuous input of woody material and the fauna may benefit from the resulting increase in detritus retention.

Keywords: forestry, detritivores, old-growth conifers, river management, woody debris

Introduction

Commercial harvesting for timber and pulpwood is a major environmental impact in forested regions of the world. In addition to perturbations caused by logging activities, much commercial forestry now depends heavily on planted monocultures, often of exotic tree species. As such, the presence of the forest itself also constitutes a potentially detrimental environmental impact. In the United Kingdom today, over 60% of woodland comprises plantations of exotic conifers, particularly the North American Sitka spruce (*Picea sitchensis* (Bong.) Carr.). Most plantations were established during the second half of the 20th Century in upland areas formerly constituting open moorland or rough grazing land, the conversion of which to forest therefore represented a major land use change. Water courses in such areas are susceptible to changes in land management wrought by large-scale plantation of trees. Hydrology, sediment yield, water chemistry and temperature have been altered (Hornung and Newson, 1986; Leeks and Roberts, 1987; Weatherley and Ormerod, 1990; O'Halloran and Giller, 1993; Ormerod *et al*., 1993), with associated adverse effects on their biota (Ormerod *et al*., 1987; Tierney *et al*., 1998).

Forestry also has an energetic impact on upland streams by altering the availability of different food sources for the stream biota. Open streams are poorly retentive of the organic matter that enters the stream from riparian vegetation and have low detrital standing stocks (Cariss and Dobson, 1997). However, they are characterised by high algal production, providing the major energy resource for primary consumers (Behmer and Hawkins, 1986). In naturally wooded streams, where primary production is suppressed by shading, the major energy resource is provided by allochthonous leaf litter whose retention is significantly enhanced by pieces of dead wood (DW) such as branches, twigs and occasionally entire trees that fall into the channel (Pozo *et al*., 1998). In conifer plantations, however, retention is low because trees are harvested before they begin to drop branches to any great extent. Therefore, plantation streams may retain the low retentive capacity of moorland streams but suffer from a reduction in algal production through heavy, permanent shading (Friberg and Kjeldsen, 1994; Friberg, 1997). A further detrimental impact is the generally low quality of conifer needles as a food resource for detritivores (Bärlocher *et al*., 1978; Graça and Pereira, 1995). If retained on the streambed for a long enough period of time, needle quality is improved by microbial conditioning and they can support large numbers of invertebrates (Grafius and Anderson, 1980). Low retention generally precludes this from occurring and as a consequence, invertebrate abundance is generally lower than in equivalent streams shaded by broadleaved woodland (Friberg *et al.*, 2002).

Management of upland streams in the United Kingdom needs to address the issue of reduced energy supply. Modern forestry practice avoids planting in the riparian zone (Forestry Commission, 1993) but, in many older plantations, the commercial crop overhangs water courses. In some sites, streamside trees have been removed to increase light inputs, but the process of removal is disruptive with minimal benefits (Ormerod *et al.*, 1993). An alternative approach may be to enhance retention capacity of impacted stream channels (Dobson *et al*., 1995; Haapala and Muotka, 1998). Ideally, this would be in the form of buffer zones removed from commercial activity (Forestry Commission, 1993; Dobson and Cariss, 1999). In practice, however, these take many years to develop, and experimental assessments of their potential effectiveness are required.

This study describes a manipulation of retention in streams running through intensive commercial forestry where inputs were dominated by low quality coniferous material and retention was predicted to be low. The aim of the study was to determine the effect of permanent retention structures on the detrital standing stock and invertebrate communities, and to assess the viability of using detritus retention as a management tool.

Methods

STUDY AREA

The Kielder Forest in Northumberland is the largest area of conifer plantation in Britain, covering around 475 km^2. The plantation is dominated by two exotic species — the most widely planted tree is Sitka spruce, while Norway spruce (*Picea abies* (L.) Karsten) dominates valley bottoms — and is managed intensively for commercial forestry. The forest ranges in altitude from 150 to 500 m and is characterised by gleyed and peaty soils. The area was previously open moorland and rough grazing ground until the onset of afforestation in 1926. The most intensive period of planting occurred between 1946 and 1960, when 200 km^2 were planted (Hibberd, 1985).

Three low order streams were used for this study (Table 1). Capon Burn and Kittythirst ran through dense (approximately 40 year old) spruce plantation, with trees planted up to the water's edge and completely overshading the channels. Steep Sike drained a spruce plantation but had a riparian zone of alder (*Alnus glutinosa* (L.) Gaertn.), under whose open canopy was an understorey of grasses.

STUDY DESIGN

In each stream, a 20 m stretch was chosen and divided into the upstream reference and downstream experimental reach (each 10 m long). All benthic samples were taken using a Surber sampler (area 0.0625 m^2, mesh size 250 μm) and the contents preserved on site with 4% formalin. Immediately before manipulation, five benthic samples were taken at random from each reach to enable a pre-manipulation comparison between reaches.

Capon Burn and Kittythirst were manipulated in April

Table 1. Summary of the sites used in this study. Conductivity and pH measurements are based on field readings taken on each sample collection date.

Site	*Grid Ref.*	*Altitude (m)*	*Stream Order*	*Mean width (m)*	*Slope (%)*	*Mean pH (range)*	*Conductivity (μS cm^{-1})*	*Riparian vegetation*
Capon Burn	NY630914	210	1	1.8	3.1	6.1 (4.2-7.6)	77	Shaded, semi-mature spruce
Kittythirst	NY609962	230	1	1.6	3.5	7.6 (7.2-8.3)	241	Shaded, semi-mature spruce
Steep Sike	NY624 890	240	1	1.2	5.0	5.5 (3.9-6.6)	56	Lightly shaded, alder buffer strip

1997; Steep Sike was manipulated in October 1997. The streams were manipulated by adding ten round logs (Sitka spruce) to the experimental reach. Each log was secured perpendicular to the flow (using four steel poles) and spaced approximately one metre apart. The logs used in the manipulation were approximately 1 m long and 0.1 m in diameter, with all side branches removed; they were harvested locally several weeks prior to manipulation and had been stored in the open prior to use. The logs were chosen for the manipulation because they were widely available and their simple structure enabled easy replication.

Following manipulation, benthic samples were taken from experimental streams at approximately three-monthly intervals until April 1999. In each reach, samples were taken from five random points, with the exception that no given point was sampled on consecutive dates. In experimental reaches, the physical structure of the manipulation and of the Surber sampler meant that samples could be taken effectively only immediately downstream of logs.

Sampling and data processing

In the laboratory, invertebrates were removed from each sample and identified to species and counted; early instar insect larvae, tipulids and chironomids were identified to genus or family. The organic matter caught in the samples was dried at 60°C for 48 h and separated into non-woody and woody fractions. The woody fraction included sticks and twigs <2 cm in diameter; larger material was omitted from the study because it was rarely caught and the scale of the study was inappropriate to assess such inputs (Campbell *et al.*, 1992). After drying, non-woody and woody fractions were weighed, burned at 550°C for 3 h and re-weighed to attain ash-free dry mass (AFDM).

DATA ANALYSIS

The primary comparison of interest was reference versus experimental reaches. Steep Sike was manipulated later than the other sites to replace a site that was unsuitable, and therefore, the experimental design was unbalanced. For this reason, data from each site were analysed separately, a strategy further justified on the grounds that the sites all showed intrinsic differences (see Table 1) which would have confounded the main comparison.

Pre-manipulation

To ensure that the reference and experimental reaches were comparable prior to manipulation, each stream was compared separately for mass of non-woody and woody detritus. The invertebrate fauna at each site was compared for total abundance and mean taxon richness per sample. In addition, species data were aggregated to compare the abundance of numerically dominant families (families which constituted over 2% of the total invertebrate assemblage at each site). These categories were analysed separately for each stream using independent samples *t*-tests. Significance levels were adjusted using a Bonferroni correction because multiple comparisons were made. Data were $\log_{10}$ (n+1) transformed where appropriate to satisfy assumptions of normality and homogeneity of variances.

Post-manipulation

Post-manipulation samples were compared using the same categories as the pre-manipulation analysis. To investigate whether the manipulation had a significant effect on detritus levels or the invertebrate fauna, two-way ANOVA was carried out with date and treatment (reference versus manipulation) as the tested variables. Data were $\log_{10}$ (n+1) transformed where required.

Results

PRE-MANIPULATION

The pre-manipulation samples taken in April 1997 for Capon Burn and Kittythirst and October 1997 for Steep Sike are summarised in Table 2. There were no significant differences between reference and experimental samples in the standing stock of detritus or DW at all three sites. In Capon Burn and Steep Sike, there were no differences in invertebrate numbers between reaches. These results indicate that the reference and manipulation reaches were similar enough prior to manipulation to be compared experimentally.

At Kittythirst, some components of the invertebrate community differed between the reference and manipulation reaches (Table 2). Total invertebrate abundance and numbers of baetid mayflies and chironomids were significantly greater in the reference reach. Because of these significant differences between the reaches before manipulation, post-manipulation results for Kittythirst should be interpreted with caution. However, it should be noted that the mass of detritus, taxon richness and abundance of numerous invertebrate families were similar enough between reaches to allow valid comparisons after manipulation.

POST-MANIPULATION

Detritus

The standing stock of non-woody detritus in the reference reach was low for all three streams (Fig. 1a). Similarly, DW was rarely found in the reference samples of each stream (Fig. 1b). At Capon Burn and Steep Sike, the manipulation

Table 2. Premanipulation comparison of reference and manipulation samples for each stream. Mean values are expressed as mass or numbers per 0.0625 m^2. Invertebrate families are listed in order of their relative abundance (%) over the duration of the study. df = 8 in all cases. Critical significance levels were adjusted (Bonferroni) to account for multiple testing; Capon Burn $\alpha = 0.006$, Kittythirst $\alpha = 0.005$, Steep Sike $\alpha = 0.006$.

	Reference Reach Mean (SD)	*Experimental Reach Mean (SD)*	*t-value*	*P*
Capon Burn				
Non-woody detritus	0.49 (0.52)	0.44 (0.24)	0.01	0.99
Woody detritus	0.0 (0.0)	0.0 (0.0)	—	—
Total invertebrates	51.4 (34.35)	47.0 (15.36)	0.01	0.99
Taxon richness	11.2 (1.3)	10.2 (3.19)	0.82	0.435
Chironomidae (25.0%)	1.8 (1.1)	1.8 (3.03)	0.74	0.480
Nemouridae (22.3%)	17.8 (9.68)	13.6 (10.43)	0.80	0.445
Leuctridae (18.8%)	7.6 (4.72)	7.8 (2.11)	0.08	0.941
Baetidae (10.78%)	3.0 (2.83)	2.0 (1.50)	0.07	0.949
Simuliidae (6.4%)	0.8 (0.84)	2.4 (4.83)	0.26	0.799
Taeniopterygidae (6.0%)	15.4 (17.59)	14.2 (11.08)	0.09	0.929
Polycentropodidae (2.4%)	1.2 (0.84)	1.2 (1.64)	0.41	0.692
Kittythirst				
Non-woody detritus	0.8 (0.46)	0.97 (0.58)	0.53	0.611
Woody detritus	0.0 (0.0)	0.0 (0.0)	—	—
Total invertebrates	126.2 (30.33)	49.8 (14.18)	5.45	<0.001
Taxon richness	20.4 (4.39)	15.8 (4.76)	1.58	0.153
Baetidae (28.1%)	56.4 (14.52)	16.6 (8.26)	5.29	<0.001
Gammaridae (17.8%)	12.2 (17.33)	2.6 (1.52)	1.36	0.212
Heptageniidae (11.2%)	10.8 (4.15)	6.8 (2.78)	1.65	0.138
Leuctridae (7.4%)	23.6 (4.98)	18.4 (7.47)	1.35	0.215
Elmidae (6.3%)	13.0 (6.52)	3.2 (3.84)	3.04	0.016
Chironomidae (5.8%)	5.0 (1.0)	1.0 (1.41)	4.05	0.004
Nemouridae (3.9%)	2.4 (1.14)	2.0 (2.55)	0.90	0.395
Simuliidae (3.7%)	0.2 (0.45)	4.6 (3.44)	3.04	0.016
Tipulidae (2.3%)	4.6 (2.07)	2.4 (1.95)	1.56	0.156
Steep Sike				
Non-woody detritus	3.67 (2.60)	3.16 (1.35)	0.04	0.973
Woody detritus	0.52 (0.83)	0.06 (0.14)	1.20	0.265
Total invertebrates	103 (37.11)	113.8 (53.72)	0.36	0.729
Taxon richness	13.8 (4.71)	15.6 (3.05)	0.88	0.402
Nemouridae (33.8%)	10.6 (9.5)	12.2 (13.92)	0.43	0.681
Leuctridae (23.0%)	30.6 (18.23)	44.4 (26.7)	1.05	0.326
Chironomidae (15.1%)	6.2 (6.3)	4.6 (2.51)	0.10	0.924
Simuliidae (7.4%)	1.8 (4.03)	0.2 (0.45)	0.67	0.522
Taeniopterygidae (5.1%)	0.8 (1.79)	0.2 (0.45)	0.52	0.615
Polycentropodidae (4.0%)	4.4 (2.97)	7.6 (4.16)	1.00	0.346
Leptophlebiidae (4.0%)	35.0 (23.89)	22.8 (10.52)	0.79	0.452

was generally slow to have an effect on retention (Fig. 1a, b). However, by August 1998 a considerable increase in detritus levels was apparent at both sites. The same general pattern was found at Kittythirst, although the increase in non-woody detritus was more pronounced in the first half of the study period than the other sites (Fig. 1a). The overall effect of the manipulation in increasing retention was highly significant for each stream, although the slow initial increases in the experimental reaches resulted in significant interaction terms in most cases (Table 3).

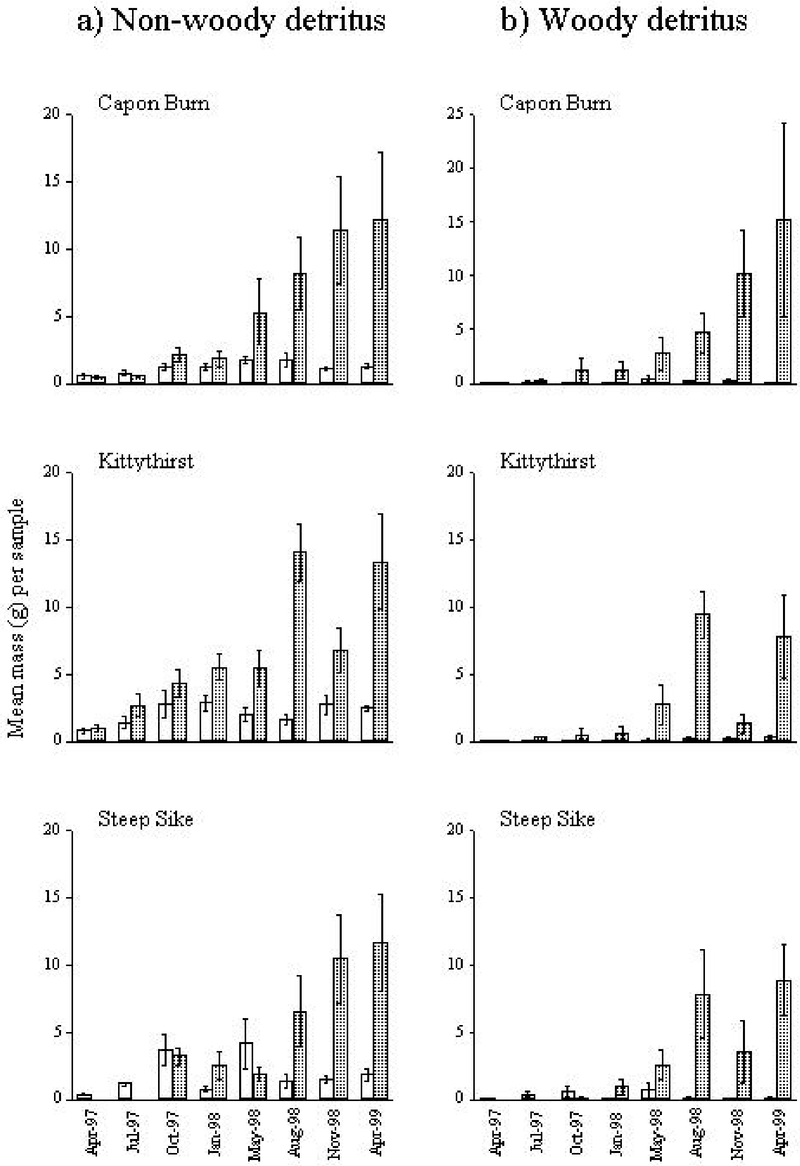

Fig. 1. *Effect of manipulation on detrital standing stock. Clear bars = reference, shaded bars = manipulation. Premanipulation samples were taken in April 1997 for Capon Burn and Kittythirst and October 1997 for Steep Sike. Vertical axes show AFDM (g) per 0.0625 m^2 ± 1SE.*

Invertebrate abundance

Overall, total invertebrate abundance and taxon richness were significantly higher in the manipulation samples relative to the references (Fig. 2; Table 4). This was true for each stream, although total invertebrate abundance at Kittythirst was a borderline exception with a *P*-value of exactly 0.05.

The most common families at each site were generally more abundant in experimental reaches than references, although chironomid numbers were higher only at Kittythirst (Table 4). Among dominant mayfly families, Baetidae at Capon Burn, Heptageniidae at Kittythirst and Leptophlebiidae at Steep Sike did not differ in abundance between reference and experimental samples. At Kittythirst, however, baetid mayflies and elmid beetles maintained the higher densities in the reference reach that had been recorded from the pre-manipulation samples. The effect of sampling date on invertebrate abundance was highly significant for most of the common taxa at each site (Table 4), probably a reflection of the seasonal patterns of adult emergence and larval recruitment associated with most aquatic insect species. Unlike mass of detritus (Table 3), however, few invertebrate taxa showed a significant date/treatment interaction (Table 4).

Discussion

All three streams studied in Kielder Forest had low detrital

Table 3. Two-way ANOVA comparing the effect of sampling date and treatment (reference vs. manipulation samples) on the mass of detritus (g $0.0625m^{-2}$) at each stream. Table shows F-values and associated probabilities.

	Effect of treatment		*Effect ofdate*		*Effect of interaction*	
	F	*P*	*F*	*P*	*F*	*P*
CAPON BURN	(df = 1,56)		(df = 6,56)		(df = 6,56)	
Non-woody detritus	53.46	<0.001	3.93	0.002	3.03	0.012
Woody detritus	52.89	<0.001	8.91	<0.001	6.39	<0.001
KITTYTHIRST	(df = 1,56)		(df = 6,56)		(df = 6,56)	
Non-woody detritus	28.79	<0.001	5.22	<0.001	3.07	0.011
Woody detritus	33.77	<0.001	3.06	0.012	2.65	0.025
STEEP SIKE	(df = 1,40)		(df = 4,40)		(df = 4,40)	
Non-woody detritus	22.20	<0.001	3.33	0.019	4.39	0.005
Woody detritus	36.64	<0.001	2.34	0.072	2.32	0.073

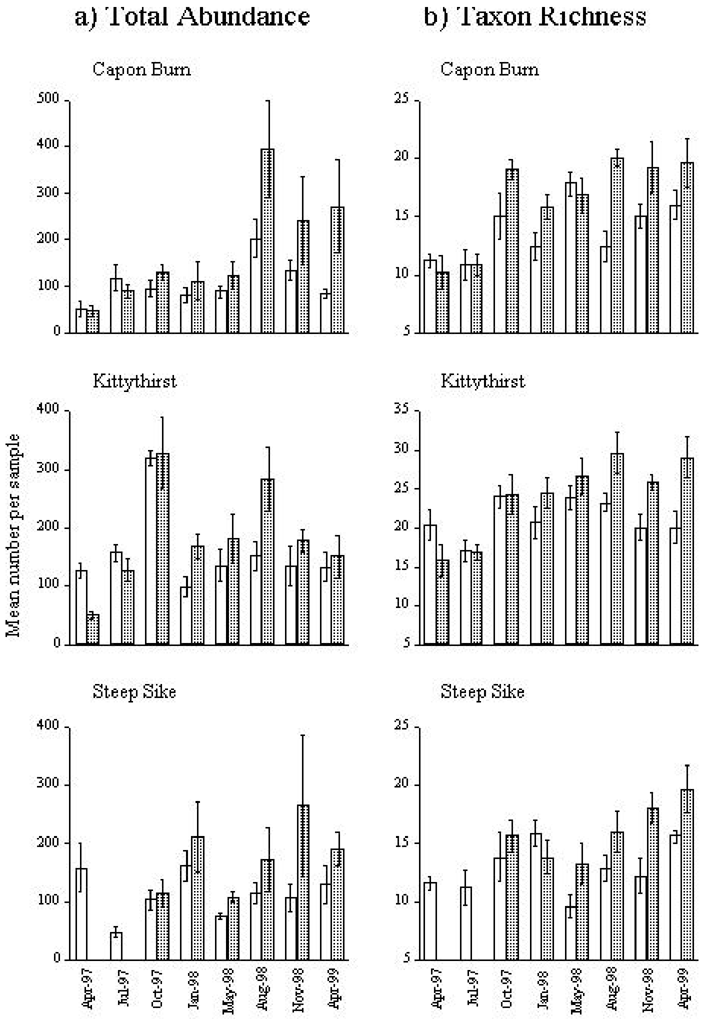

Fig. 2. Effect of manipulation on invertebrate abundance and taxon richness. Clear bars = reference, shaded bars = manipulation. Premanipulation samples were taken during April 1997 from Capon Burn and Kittythirst and October 1997 from Steep Sike. Vertical axes show numbers per 0.0625 m^2 ± 1SE. Note different scales on vertical axes.

Table 4. **T**wo-way ANOVA comparing the effect sampling date and treatment (reference vs. manipulation samples) on the invertebrate abundance and taxon richness at each stream. Table shows F-values and associated probabilities.

	Effect of treatment		*Effect of date*		*Effect of interaction*	
	F	*P*	*F*	*P*	*F*	*P*
CAPON BURN	(df = 1,56)		(df = 6,56)		(df = 6,56)	
Total invertebrates	5.36	0.024	4.38	0.001	0.86	0.530
Taxon richness	15.36	<0.001	6.94	<0.001	1.86	0.104
Chironomidae	1.12	0.230	2.67	0.024	0.97	0.455
Nemouridae	13.13	0.001	25.58	<0.001	1.56	0.175
Leuctridae	4.93	0.030	6.46	<0.001	2.27	0.050
Baetidae	4.98	0.487	42.75	<0.001	0.62	0.716
Simuliidae	10.94	0.002	60.22	<0.001	1.55	0.180
Taeniopterygidae	0.44	0.508	43.79	<0.001	0.73	0.631
Polycentropodidae	0.04	0.847	8.19	<0.001	0.32	0.927
KITTYTHIRST	(df = 1,56)		(df = 6,56)		(df = 6,56)	
Total invertebrates	4.02	0.050	5.62	<0.001	1.25	0.294
Taxon richness	13.76	<0.001	6.00	<0.001	1.48	0.201
Baetidae	7.44	0.009	7.36	<0.001	1.19	0.324
Gammaridae	8.70	0.005	5.16	<0.001	1.05	0.406
Heptageniidae	1.77	0.189	52.03	<0.001	2.50	0.032
Leuctridae	14.14	<0.001	5.98	<0.001	1.94	0.090
Elmidae	9.77	0.003	2.26	0.050	1.56	0.176
Chironomidae	66.40	<0.001	29.62	<0.001	3.04	0.012
Nemouridae	9.85	0.003	9.35	<0.001	1.31	0.270
Simuliidae	12.94	<0.001	3.54	0.005	0.23	0.965
Tipulidae	0.03	0.955	3.30	0.008	1.40	0.232
STEEP SIKE	(df = 1,40)		(df = 4,40)		(df = 4,40)	
Total invertebrates	5.99	0.019	1.76	0.156	0.49	0.746
Taxon richness	10.04	0.003	5.45	0.001	2.29	0.076
Nemouridae	18.99	<0.001	29.57	<0.001	1.99	0.115
Leuctridae	7.21	0.011	5.15	0.002	0.16	0.957
Chironomidae	2.37	0.132	57.78	<0.001	0.17	0.953
Simuliidae	4.45	0.041	8.46	<0.001	0.19	0.945
Taeniopterygidae	0.24	0.628	31.52	<0.001	0.31	0.870
Polycentropodidae	0.02	0.966	5.77	<0.001	0.06	0.993
Leptophlebiidae	0.01	0.949	13.01	<0.001	1.09	0.373

standing stocks in their reference reaches, more characteristic of open moorland streams (e.g. Dobson *et al*., 1995; Cariss and Dobson, 1997) than forest streams. Values recorded from wooded streams are generally in excess of 100 gm^{-2} (e.g. Wallace *et al*., 1995b; Marxsen *et al*., 1997; Smock, 1997) compared with an average from Kielder Streams of 32 gm^{-2}. Interestingly, the difference in background detrital standing stocks between Kielder and other wooded streams was not simply an effect of conifer trees, as evidenced by the equally low retention in Steep Sike where the riparian zone was dominated by alder trees.

Addition of logs successfully enhanced detritus retention on the streambed in all three manipulated streams. Increases were most apparent in the second half of the study period; indeed, analysis of the first year alone revealed little increase (Pretty and Dobson, 2001). The slow initial response was probably due to the nature of the DW added. For the purpose of easy replication, the logs used were of a uniform shape and size with all side branches removed. It was expected that they would quickly accumulate small sticks and branches that would further enhance retention. However, the smooth, round shape of the logs meant they were slow to catch DW and the main retention feature was the steel poles that held the logs in place. Despite the slow response, the wood-pole manipulation became more effective over time with the amount of detritus retained being greater in the second year of the study (Fig. 1). More complex structures, like natural woody inputs with side branches, would presumably retain detritus more rapidly.

Despite the low natural levels of detritus, the invertebrate fauna in the Kielder streams was dominated by detritivores. This raises questions about their dependence upon a detrital food source, and it is becoming increasingly well documented that many stream invertebrates are opportunistic feeders. For instance, feeding plasticity has been demonstrated for detritus-feeders such as amphipods and trichopterans (e.g. Winterbourn *et al*., 1985; Friberg and Jacobsen, 1994; Mihuc and Mihuc, 1995). Similarly, Ledger and Hildrew (2000) found that nemourid stoneflies could effectively graze epilithic biofilm as an alternative to allochthonous detritus. It is likely, therefore, that feeding plasticity may have assisted the large detritivore populations present in the Kielder streams. Regardless, invertebrate assemblages clearly benefited (in terms of numbers and species richness) from the increased availability of detritus, and the positive response was strongest among groups typically regarded as detritivores (e.g. Nemouridae and Leuctridae). Despite this response, there was no evidence for an increase in invertebrate abundance over time as the retention structures became more efficient. Therefore, the log-pole addition may have increased numbers of invertebrates not simply by enhancing a specific resource but by a general manipulation of the streambed habitat. Logs acted as stabilising influences on the channel, and their influence on physical and hydraulic characteristics may have been their most important effect. For example, similar log-addition experiments altered local current velocities, redistributed channel substrata and promoted the formation of pools (Hilderbrand *et al*., 1997; Wallace *et al*., 1995a; Lehane *et al*., 2002). Such changes to stream morphology may contribute to habitat heterogeneity/complexity and influence invertebrate community structure and secondary production (Wallace *et al*., 1995a; Lemly and Hilderbrand, 2000).

In this study, the addition of logs resulted in a general increase in invertebrate numbers and also in taxon richness. Furthermore, there was no evidence for the manipulation having a detrimental influence on any component of the fauna. Therefore, using several criteria, the manipulation appeared to enhance the invertebrate community of the study streams. The study may underestimate the full effect of log-pole addition, as practical constraints meant that samples from the manipulated reach were taken immediately downstream of logs, whereas their greatest influence on detritus aggregation was probably immediately upstream (Wallace *et al*., 1995a).

It is possible that enhanced numbers were an artefact created by the redistribution of invertebrates already present in the experimental reach, rather than a genuine increase in invertebrate populations. Such aggregations could occur through active foraging as well as by drifting invertebrates accumulating in 'dead zones' created by the manipulation (*cf* Lancaster and Hildrew, 1993; Lancaster, 1999). Whilst such small-scale movements undoubtedly occur (Winterbottom *et al*., 1997), invertebrates are quick to colonise free space and it is unlikely that areas between traps would remain depleted for long. There is also evidence that increasing detrital food sources could enhance overall invertebrate production (Richardson, 1991; Richardson and Neill, 1991; Basset and Glazier, 1995). If this were to benefit adult fecundity (larger females may carry more eggs) there is potential for enhanced recruitment in the next generation. A further potential role of the detritus accumulations is as oviposition sites. Circumstantial evidence from Capon Burn supported this idea; here detritus accumulations contained many young nemourid larvae relative to the natural substrate (J.L. Pretty, *pers. obs.*). However, further research would be necessary to demonstrate whether this association was due to oviposition or invertebrate drift.

MANAGEMENT IMPLICATIONS

Clearly this study was relatively short term and carried out over a small spatial scale. It does, however, contribute valuable information to the debate on management of streams running through commercial plantations. In the United Kingdom, the Forestry Commission has produced management guidelines that recommend leaving open or lightly-shaded buffer zones between the stream and the planted trees (Forestry Commission, 1993). These buffer zones are valuable in maintaining invertebrate diversity (e.g. Rundle *et al*., 1992; Ormerod *et al*., 1993) and are probably the most appropriate management strategy for such systems. While replacing such a management strategy in favour of heavily shaded streams is not advocated here, allowing streamside trees to mature may be the best option in some circumstances. Many riparian areas, planted before buffer zones were common practice, now support mature trees. The removal of trees simply to create an open buffer zone would involve major disturbance to the detriment of the stream fauna. Rather than create an open environment within the plantation, it may, therefore, be more viable to adopt a 'do nothing' approach and allow the riparian zone to mature, senesce and regenerate naturally (Dobson and Cariss, 1999). The creation of old growth forest (trees >100 years old) has been recognised as an important strategy to enhance the conservation value of plantation forests, for both aquatic and terrestrial species (Peterken, 1996). Furthermore, Peterken *et al*., (1992) suggest that old growth would ideally be situated on the lower slopes of valleys, where wind damage is reduced and soil and microclimate are more favourable. This strategy is not entirely compatible with current Forestry Commission guidelines, but patches of old growth forest along river margins could complement open buffer zones and maximise habitat heterogeneity within an area of commercial forestry.

By definition, old growth forest takes time to develop. However, its most important effect on streams — input of DW — can be simulated. Detritus manipulation studies using retention devices to enhance standing stocks have now been carried out in numerous streams covering a range of water chemistry features and riparian vegetation types (Dobson and Hildrew, 1992; Dobson *et al*., 1995; Murphy and Giller, 2000; Muotka and Laasonen, 2002; this study). In all of these studies, increased detrital standing stocks have been achieved easily and at least some components of the invertebrate fauna responded positively to the increase in detritus availability, suggesting that the method is fairly robust. In addition, activity of aquatic hyphomycete fungi increases when detritus levels are artificially enhanced (Laitung *et al*., 2002); this will increase rates of conditioning and improve the quality of the detritus retained as a food resource for detritivores. Therefore, if riparian areas of forestry are to be removed from the commercial sphere, their positive effects on streams can be accelerated by simple channel manipulation, like the type described here. This change will enhance stream productivity and, if the results from this study are generally applicable, increase species richness, particularly benefiting less common species. Furthermore, the manipulation requires little maintenance, making it a cost-effective form of management. In due course, as trees reach the old growth stage, inputs of wood will occur naturally, thus removing the requirement for further management.

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